# TAXONOMIC REVISION OF THE AUSTRALIAN LIZARD *PYGOPUS NIGRICEPS* (SQUAMATA: GEKKONOIDEA)

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Allozyme electrophoresis and analysis of scalation, colour pattern and body proportions were used to define species boundaries in the widespread, arid adapted legless lizard *Pygopus nigriceps*. Three species are recognised. *Pygopus nigriceps* (Fischer, 1882) is confined to the sandy deserts of central and western Australia. *Pygopus schraderi* Boulenger, 1913 inhabits mainly heavier soils and rocky substrates in the arid and semi-arid zones of eastern Australia. The third species is described as new, and occurs in the wet-dry tropics of northern Australia.

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Pygopods are a lineage of snake-like lizards endemic to Australia and New Guinea with evolutionary affinities to the geckoes (Kluge 1987; King 1990; Donnellan *et al.* 1999). There are 35 species of pygopods recognised, placed by most recent authors into eight genera (Kluge 1974, 1976; Wilson & Knowles 1988; Storr *et al.* 1990; Ehmann 1992; Cogger 1996). The genus *Pygopus* Merrem is considered (Kluge 1974; Cogger 1996) to comprise two species, *Pygopus lepidopodus* (Lacépède) which occupies the southwestern, southern and eastern margins of Australia, and *Pygopus nigriceps* (Fischer) which is widespread throughout the more xeric parts of Australia.

Kluge (1974) found considerable phenotypic divergence between populations of *P. nigriceps* from the western and eastern parts of Australia. They were separated by a narrow zone of character discontinuity located approximately along 135°E. In addition, he found that specimens from north of 18°S in Western Australia (WA) and the Northern Territory (NT) tended to be more like the eastern than the western form but Kluge had insufficient specimens to be able to identify the northern extension of the character discontinuity. He suggested that two subspecies be recognised, a western *P. n. nigriceps* and an eastern *P. n. schraderi* Boulenger, and that the northern specimens be treated as a taxonomically separate unnamed, problematical set.

Kluge's separation of *P. nigriceps* into two subspecies was continued by Storr *et al.* (1990) and Cogger (1996) who both ascribed the northern WA and NT specimens to *P. n. schraderi*. Wilson and Knowles (1988) suggested that northern populations were an intermediate form that could be tentatively regarded as undescribed. Ehmann (1992, 1995) provided two different interpretations for the status of *P. nigriceps*. In 1992, he suggested there were two separate species, *P. nigriceps* whose range he gave approximately as west of 135°E, including northern WA and the NT, and *P. schraderi*, whose range he gave approximately as east of 135°E including Cape York Peninsula. However, by 1995 he had altered this view and suggested there were two subspecies, *P. n. nigriceps* and *P. n. schraderi*. Their ranges were as he had suggested previously for *P. nigriceps* and *P. schraderi*, except that populations from northern WA and the NT were assigned to *P. n. schraderi* while those from Cape York Peninsula were not assigned to either subspecies.

In the present study, we have employed multilocus allozyme electrophoresis and morphology to examine the taxonomic status of *P. nigriceps* and to clarify species boundaries. This revision explicitly invokes the evolutionary species concept (Simpson 1951), the significant feature of which is that a species is a lineage evolving separately from others and with its own unitary evolutionary history and fate.

## Materials And Methods

### Specimens

For the allozyme analysis, frozen liver samples from the Australian Biological Tissue Collection (ABTC) at the South Australian Museum, Adelaide were used. The samples had been dissected from fresh specimens and stored continuously at –80°C. In all, liver samples from 43 specimens of *P. nigriceps* were available for analysis. In addition, liver samples from nine specimens of *P. lepidopodus*, chosen to cover the known range, were used to provide a sister lineage for the *P. nigriceps* species-complex, and as a check on the authenticity of the *P. nigriceps* samples. An incidental aim was to gain preliminary data on possible cryptic speciation, given the extensive range and known colour variations in *P. lepidopodus*.

There was the potential for a very large number of *P. nigriceps* specimens to be available for morphological analysis from the Australian state museum collections. We concentrated on specimens from north of the Tropic of Capricorn (23°26'30"S). All specimens whose liver tissues were examined in the allozyme study were examined for morphological characters, provided that the body was available for analysis, as were all specimens in the South Australian Museum collection and selected specimens from the other state museums. Museum registration numbers for all specimens examined electrophoretically and/or morphologically (*n* = 260) are given in the Appendix. Institutional acronyms follow Leviton *et al.* (1985).

### Allozyme electrophoresis

Allozyme electrophoresis was conducted with liver homogenates on cellulose acetate gels (Cellogel, Chemetron) according to the methods of Richardson *et al.* (1986). Proteins and enzyme products of 35 presumed loci were scored. The enzymes and other products stained, abbreviations and Enzyme Commission Numbers are: aspartate aminotransferase (AAT, EC 2.6.1.1), aconitate hydratase (ACOH, EC 4.2.1.3), aminoacylase (ACYC, EC 3.5.1.14), adenosine deaminase (ADA, EC 3.5.4.4), alcohol dehydrogenase (ADH, EC 1.1.1.1), carbonate dehydratase (CA, EC 4.2.1.1), diaphorase (DIA, EC 1.6.99.?), enolase (ENO, EC 4.2.1.11), esterase (EST, EC 3.1.1.?), fructose-bisphosphatase (FBP, EC 3.1.3.11), fumarate hydratase (FUMH, EC 4.2.1.2),

glyceraldehyde-3-phosphate dehydrogenase (GAPDH, EC 1.2.1.12), guanine deaminase (GDA, EC 3.5.4.3), (S)-2-hydroxy-acid oxidase (GOX, EC 1.1.3.15), glycerol-3-phosphate dehydrogenase (G3PDH, EC 1.1.1.8), glucose-6-phosphate isomerase (GPI, EC 5.3.1.9), β-glucuronidase (βGLUR, EC 3.2.1.31), L-iditol dehydrogenase (IDDH, EC 1.1.1.14), isocitrate dehydrogenase (IDH, EC 1.1.1.42), cytosol aminopeptidase (LAP, EC 3.4.11.1), L-lactate dehydrogenase (LDH, EC 1.1.1.27), lactoglutathione lyase (LGL, EC 4.4.1.5), malate dehydrogenase (MDH, EC 1.1.1.37), 'malic' enzyme (MDHP, EC 1.1.1.40), mannose-6-phosphate isomerase (MPI, EC 5.3.1.8), nucleoside-diphosphate kinase (NDPK, EC 2.7.4.6), dipeptidase (PEP-A, EC 3.4.13.?), tripeptide aminopeptidase (PEP-B, EC 3.4.11.?), proline dipeptidase (PEP-D, EC 3.4.13.?), phosphogluconate dehydrogenase (PGDH, EC 1.1.1.44), phosphoglucomutase (PGM, EC 5.4.2.2), superoxide dismutase (SOD, EC 1.15.1.1) and triose-phosphate isomerase (TPI, EC 5.3.1.1). For the genetic analysis, geographically proximate specimens of a single genetic type that is, where there were no fixed allelic differences, were pooled to form Operational Taxonomic Units (OTUs). On this basis, 25 OTUs of *P. nigriceps* were designated. Each of the *P. lepidopodus* specimens was treated as a separate OTU. The OTU localities are shown in Fig. 1 and composition in the Appendix. Evolutionary distances between OTUs were estimated with Cavalli-Sforza chord distances (Cavalli-Sforza & Edwards 1967) calculated with BIOSYS-1 (Swofford & Selander 1981). The Neighbour-joining (NJ) algorithm, implemented in PHYLIP version 3.5c (Felsenstein 1993) was used to build trees from these distances. The maximum parsimony (MP) criterion optimality was also used to recover phylogenetic trees with each locus considered as a character and each allele as an unordered character state. Polymorphic loci were encoded as uncertainties using this option for multistate characters in PAUP* version 4.0b3. (Swofford 1999). The data were bootstrapped to assess confidence for individual nodes.

### Morphology

Kluge (1974) assembled a large character set for morphological analysis of the pygopods. Many of these characters are not applicable to the genus *Pygopus* and some are difficult to score in that they depend upon arbitrary starting points or locations on the body. Initially, we selected those
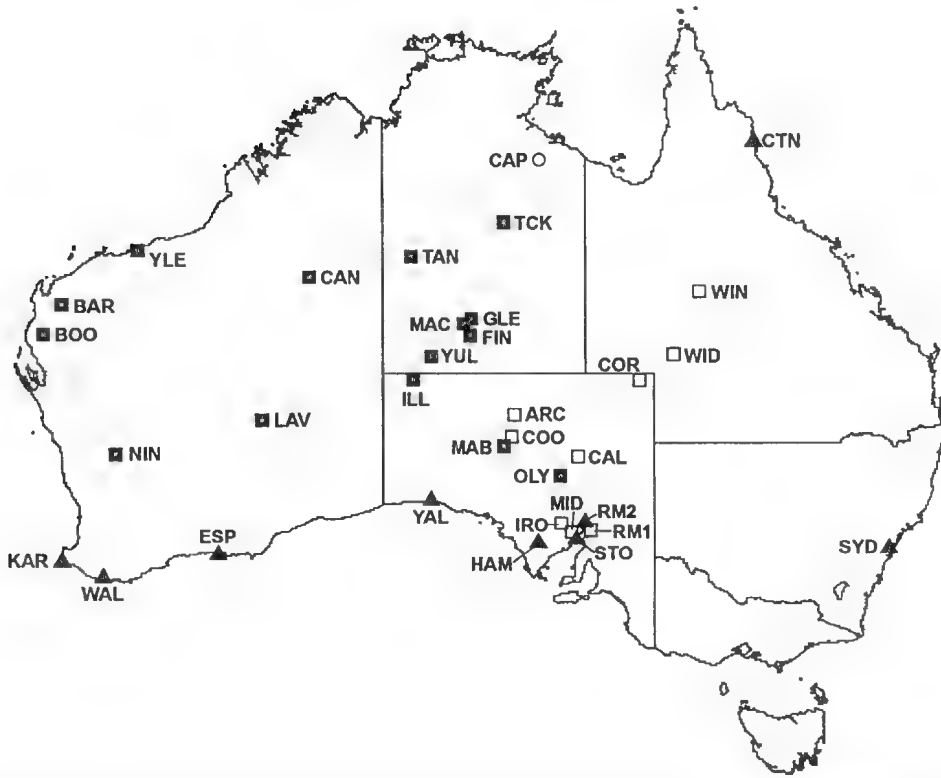
FIGURE 1. Map showing collection localities for the 34 *Pygopus* OTUs examined electrophoretically. See Appendix 1 for a key to the OTU labels. □ = 'eastern' group, ○ = 'northern' group, ■ = 'western' group, ▲ = *P. lepidopodus*.

characters reported by Kluge as varying significantly within *Pygopus* and were either quantitative in nature, or if qualitative, defined by unambiguous reference points. We added several new characters that seemed likely to be useful for taxonomic purposes. Measurements were made with vernier callipers to the nearest mm.

The characters and their abbreviations used in the morphological study are listed below. Where characters were defined by Kluge (1976), they are indicated by *; characters modified from those used by Kluge are indicated by #.

Subnostril scale# (SNS). The nostril may contact the first supralabial scale (0) or a thin strip of the nasal scale may separate the nostril from the supralabial (1). Kluge's 'subnostril scale' refers to the portion of the nasal underlying the nostril.

Ventral scales* (VS). The number of ventral scales between the posterior edge of the mental and the vent, including the preanal scale.

Orbital scales# (OS). The number of scales along the anterior margin of the bony portion of the orbit between the anteriormost and posteriormost enlarged supraciliary scales.

Dorsal scale keeling# (DSK). Keels absent (0), scales weekly keeled (1), or scales moderately keeled (2). The keeled scales were always unicarinate.

Dorsal scale row keeling (DSRK). The number of dorsal rows of scales exhibiting keeling.

Preanal pores* (PP). The total number of preanal pores.

Dorsal interorbital pattern# (DIP). Pattern on the dorsal surface of the head between the orbits. Varies from no significant pigmentation to a mottled appearance, not distinctly different from the snout, to the presence of brown or black pigmentation forming a faint to strongly contrasting dark bar. Scored as no significant pigmentation, not distinctly different from snout (0), mottled appearance not distinctly different from snout (1), brown or black pigmentation present as a faint bar (2), or

TABLE 1. Allele frequencies expressed as a percentage for 34 OTUs of *Pygopus* at 35 loci. Alleles are designated alphabetically, with 'a' being the most cathodally migrating allele. Where enzymes are encoded by more than one locus, the loci are designated numerically in order of increasing mobility. Sample sizes are given at the head of each column, except when fewer individuals were successfully typed. In the latter case sample sizes are indicated by the number in superscript beside the first allelic frequency entry for a locus. Where allele frequencies are not given, the OTU is fixed for the allele. The following loci were invariant: *Ca, βGlur, Ldh-1, Ldh-2, Lap, Mdh* and *Tpi*.

| | 'eastern' | | | | | | | | | 'northern' | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Locus | WIN 1 | WID 2 | COR 1 | COO 1 | ARC 1 | CAL 1 | MID 1 | IRO 1 | RM1 2 | CAP 3 | TCK 3 | TAN 1 | GLE 1 | FIN 1 | MAC 2 | YUL 2 |
| *Aat* | a | a | a | a | a | a | a | a | a | a | d(17) c(33) b(17) a(33) | a | a | c(50) a(50) | c(25) a(75) | c(25) a(75) |
| *Acoh-1* | b | b | b | b | b | b | b | b | b | b | a | a | b(50) a(50) | b(50) a(50) | c(50) a(50) | b |
| *Acoh-2* | c | c | d(50) c(50) | c | c | b | b | c(50) b(50) | c | a | b(83) a(17) | b | b | c | b1 | c(50) b(50) |
| *Acyc* | b | b | b | b | c(50) b(50) | c(50) b(50) | b | c | c(75) b(25) | d | b | b | b | b | b | b |
| *Ada* | a | a | a | a | a | a | a | a | a | b | b | b | b | b | b | b |
| *Adh* | a | a | a | a | a | b(50) a(50) | a | a | a | a | a | a | a | a | a | a |
| *Dia* | b | b | b | a | a | b | b(50) a(50) | b | b | a | c | c | c | c | c | c |
| *Eno* | b | b(50) a(50) | b | b | b | b | b | b | b | b | b(67) a(33) | b | b | b | b | b |
| *Est* | c(50) | b b(50) | b | b | b | b | b | b | b | b(83) | b a(17) | b | b | b | b | b |
| *Fbp* | a | a | a | a | a | a | a | a | a | a | a | a | a | a | b(25) a(75) | a |
| *Fumh* | b | b | b | b | b | b | b | b | b | b | b | b | b | b | b | b(75) a(25) |
| *Gapdh* | b | b | b | b | -- | -- | b | b | b | b | b | -- | b | b | b | b |
| *Gda* | a | a | a | a | a | a | a | a | a | b(17) a(83) | b | b | b | b | b | b |
| *Gox* | b | b | b | b | b | c(50) b(50) | b(50) a(50) | c | b | c(83) b(17) | c(83) b(17) | c | c | c | c(25) b(75) | c |
| *G3pdh* | b | b | b | b | b | b | b | b | b | a | b | b | b | b | -- | b |
| *Gpi* | a | a | a | a | -- | -- | a | a | a | a | a | a | a | a | a | a |
| *Iddh* | c | c | c | c | c | c | c | c | c | c | f | f | e | f(50) e(50) | -- | f(50) e(50) |

| 'western' | | | | | | | | | *P. lepidopodus* | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ILL 1 | OLY 3 | MAB 7 | LAV 2 | NIN 1 | CAN 1 | BAR 2 | BOO 1 | YLE 1 | YAL 1 | ESP 1 | HAM 1 | STO 1 | SYD 1 | WAL 1 | KAR 1 | RM2 1 | CTN 1 |
| c(50) a(50) | c(17) a(83) | c(36) a(64) | c(25) a(75) | a | a | a | c(50) a(50) | | a | a | a | a | a | c(50) a(50) | a | a | a |
| – | b | c(25) b(75) | b | b | – | c(25) b(50) a(25) | b | b | c | c | c | c(50) b(50) | a | c | c | c | c |
| – | b | c(14) b(86) | c(25) b(75) | b | – | c(50) b(50) | b | c(50) b(50) | e(50) d(50) | e(50) c(50) | d(50) c(50) | d | c | d | d | d | c |
| – | b | b | b | b | – | b | b | b | b | b | b | b | b | b | b | b | a |
| b | b | c(7) b(93) | b | b | – | b | b | b | – | b | b | b | b | c(50) b(50) | c(50) b(50) | b | b(50) a(50) |
| – | a | a | a | a | – | a | a | a | a | a | a | b | a | a | a | b(50) a(50) | b |
| – | c | c | c | c | – | c | c | c | – | d | d | d | d | d | d | d | c |
| b | b(33) a(67) | b(86) a(14) | b | b | b | a | a | b | c | b | c | c | a | c | c | c | a |
| b | b | b | b | b | b | b | b | b | b | b | b(50) | b a(50) | b | b | b | a | b |
| a | a | a | a | a | – | a | a | a | b(50) a(50) | a | a | a | a | b | b | a | a |
| b | b(83) a(17) | b(86) a(14) | b | b | – | b | b | b | b | b | b | b | b | b | b | b | b |
| b | b | b | b | b | – | b | b | b | a | a | a | a | a | – | – | a | a |
| – | b | b | b | b | – | b | b | b | b | b | b | b | b | b | b | b | b |
| – | d(25) c(50) | d(22) c(57) b(25) | c | c | – | c(75) b(25) | c | – | b | c | b | b | c(50) b(50) | – | – | c | c |
| | | b(21) | | | | | | | | | | | | | | | |
| – | b | b[6] | b | b | – | b | b | b | – | b | b | c | a | -- | – | b | a |
| a | a | a | a | a | a | a | a | a | a | a | a | a | a | a | a | a | b |
| f(50) e(50) | g(8) f(50) | f(25)[6] e(75) e(42) | f | – | – | f[1] | f | f | c | c(50) b(50) | b | c(50) b(50) | d | – | – | c | a |

TABLE 1.  (cont.)

| Locus | 'eastern' | | | | | | | | | 'northern' | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | WIN 1 | WID 2 | COR 1 | COO 1 | ARC 1 | CAL 1 | MID 1 | IRO 1 | RM1 2 | CAP 3 | TCK 3 | TAN 1 | GLE 1 | FIN 1 | MAC 2 | YUL 2 |
| Idh-1 | a | a | a | a | a | a | a | a | a | a | a | a | a | a | a[1] | a |
| Idh-2 | b | b | b | b | b | b | b | b | b | b | b | b | b | b | b | b |
| Lgl | b | b | b | b | b | b | b | b | b | b | b | b | b | b | b | b |
| Mpi | c | c(75) | d(50) b(25) | b c(50) | b | b | b | b | b | d | b | b(50) | b a(50) | b | b | b |
| Ndpk | b | b | b | b | b | b | b | b | b | b | b | b | b | b | b | b |
| Pep-A | | a | a | a | a | a | a | a | a | b(75) | b a(25) | c | b | b | c(50)[1] | b b(50) |
| Pep-B1 | | a | a | a | a | a | a | a | a | a | b | a | a | a | a[1] | a |
| Pep-B2 | c(50) b(50) | b | b | d | e | b | d | d | d | c(50) b(33) a(17) | c | f(50) c(50) | c | c(50) b(50) | f(50) c(25) b(25) | c |
| Pep-D | c(50) b(50) | e(50) d(50) | e(50) a(50) | e | e | e | e | e | e | e(67) c(33) | g(17) f(83) | f(50) b(50) | g(50) f(50) | g(50) f(50) | f | g(25) f(75) |
| Pgm | a | a | a | a | a | a | a | a | a | a | a | a | a | a | c(25) | a a(75) |
| Sod | c | c | c | c | c | c | c | c | c | b | c(83) b(17) | c | c | c | c | c |

brown or black pigmentation present as a strong bar (3).

Dorsal nuchal pattern* (DNP). The pattern on the dorsal surface of the head and neck immediately posterior to the parietal region varies in a similar way to the interorbital region. Scored as no significant pigmentation not distinctly different from snout (0), mottled appearance not distinctly different from snout (1), brown or black pigmentation present as a faint band (2), or brown or black pigmentation present as a strong band (3).

Orbital patch (OP). Dorsoventrally orientated darkly pigmented patch around and/or below the orbit extending to the supralabial scales and sometimes to the infralabial scales. Scored as absent (0), faint (1), moderately intense (2) or intense (3).

Narial patch (NP). Dorsoventrally oriented darkly pigmented patch or streak around and/or below the nostril extending to the supralabial scales and sometimes to the infralabial scales. Scored as absent (0), faint (1), moderately intense (2) or intense (3).

Contrast of lateral head pattern (LHP). Relative intensities of the orbital and narial patches may vary. Whereas some specimens or species show an equally intense development of both patches, others may have a noticeably weak expression of the narial patch (even absence) compared to the orbital patch. The converse (narial patch more strongly developed than orbital patch) was not observed. Scored as intensities of both patches equal (1), differing by one on the NP and OP scores (2), differing by two (3), or differing by three (4).

Snout-vent length* (SVL). The horizontal distance between the median anterior-most extreme of the snout and the median posterior-most extreme of the middle preanal scale.

These characters were scored for each specimen from which liver samples had been taken for

| 'western' | | | | | | | | | *P. lepidopodus* | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ILL 1 | OLY 3 | MAB 7 | LAV 2 | NIN 1 | CAN 1 | BAR 2 | BOO 1 | YLE 1 | YAL 1 | ESP 1 | HAM 1 | STO 1 | SYD 1 | WAL 1 | KAR 1 | RM2 1 | CTN 1 |
| — | a | a | — | a | — | a | a | a | — | a | a | a | b(50) a(50) | — | b(50) a(50) | a | a |
| — | b | c(7) b(93) | b | b | b | b | b | b | — | a | a | a | a | a | a | a | a |
| b | b | b(86) a(14) | b | b | — | b | b | b | b | b | b | b | a | — | — | b | a |
| b | b | b | b | c(50) b(50) | b | b | c(50) b(50) | b | b | b | b | b | b | b | b | b | b |
| b | b | b[6] | b | b | b | b | b | b | b | b | b | a | c | c | c | b | b |
| c(25) b(75) | c(33) b(67) | b[6] | b | b | — | b | b | b | b | b | b | b | b | — | b | b | a |
| a | c(83) a(17) | a | b(25) a(75) | c(50) a(50) | — | c(25) b(75) | b(50) a(50) | a | — | a | a | a | a | c(50) a(50) | a | a | a |
| c | c | f(21) c(79) | c | c | — | c | c | c | — | — | — | — | — | — | — | — | — |
| — | f | h(7) f(86) e(7) | g(50) e(25) | f | g | g(25) f(50) b(25) | g(50) f(50) | f e(25) | — | f(50) b(50) | c | b | f | f | e | b | f(50) c(50) |
| a | a | a | a | a | a | b(50) a(50) | a | a | a | a | a | a | a | a | a | a | a |
| c | c | c | c | c | c | c | c | c | a | a | a | a | a | a | a | a | a |

allozyme electrophoresis, except for three 'western' specimens for which vouchers were not available for examination (ABTC 6588, 31799, 31812). For statistical comparisons of the morphological characters except SVL, the significance of differences between taxa was assessed with the non-parametric Mann-Whitney *U* test. For comparisons of SVL, unpaired Student's *t* tests were used after testing for departures from a normal distribution for each taxon (Shapiro-Wilks test) and pairwise tests of equality of variances (Levene test). All tests were two-tailed with an *a* set at 0.05 and were carried out with STATISTICA (Statsoft Inc. 1997).

## Results

Table 1 shows the allelic profiles of the 25 OTUs of *P. nigriceps* and nine OTUs of *P. lepidopodus* for the 35 loci. These data were converted into matrices of percentages of loci showing fixed allelic differences (FD) and Cavalli-Sforza chord distances between OTUs (not shown). A fixed allelic difference occurs at a locus when the two samples under comparison share no alleles (Richardson *et al.* 1986). Richardson *et al.* (1986) argued that percentage of loci showing fixed allelic differences is an appropriate genetic distance metric for species boundary studies and is relatively unaffected by small sample size. We present a phenogram constructed from Cavalli-Sforza chord distances between OTUs by NJ (Fig. 2A). A heuristic search under MP found 77 335 equally most parsimonious trees of length 53 steps. A strict consensus of the equally most parsimonious trees with bootstrap proportions from 10 000 pseudoreplicates is presented in Fig. 2B. For the NJ and MP analyses adjacent populations between which there were no fixed allelic differences were pooled and allele frequencies recalculated, making
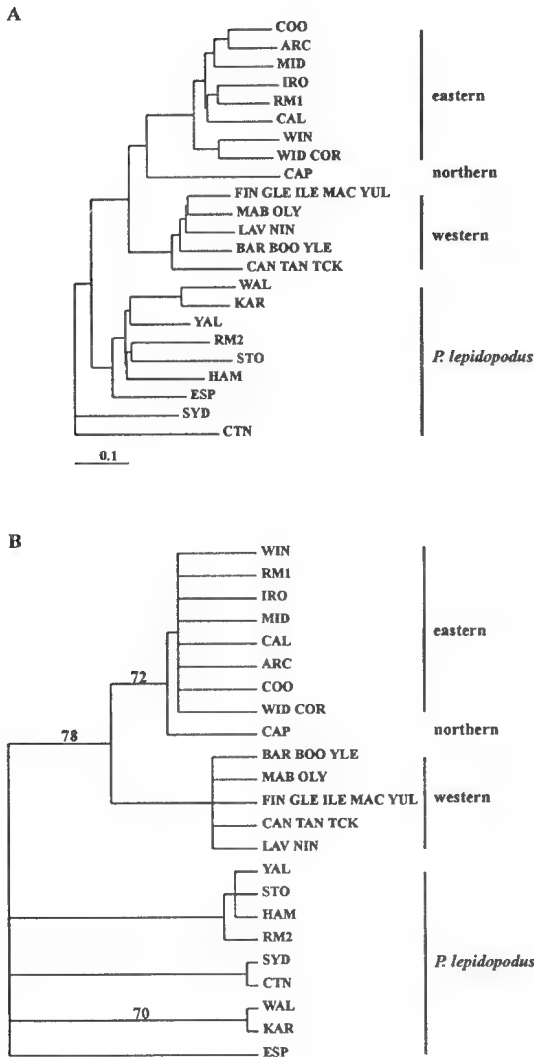
FIGURE 2. (A) A Neighbour-joining phenogram constructed from Cavalli-Sforza chord distances between OTUs; and (B) a strict consensus tree of more than 2000 equally most parsimonious trees found with a heuristic search. Bootstrap proportions >70% from 2000 pseudoreplicates are indicated to the left of relevant nodes.

a total of 14 OTUs within *P. nigriceps* for the final analyses.

The allozyme data (Fig. 2 and Table 1) show that the *P. nigriceps* OTUs are genetically more similar to one another than they are to any of the *P. lepidopodus* OTUs. Monophyly of the *P. nigriceps* OTUs received strong support (78%)

from bootstrapping (Fig. 2B). The *P. lepidopodus* OTUs exhibit considerable genetic heterogeneity suggesting that more study is warranted.

Within *P. nigriceps*, both the NJ and the MP analyses are concordant in showing the presence of three lineages herein designated 'eastern', 'northern', and 'western'. However, strong bootstrap support (>70%) was found only for the monophyly of the 'eastern' lineage (Fig. 2B). The primary split between the *P. nigriceps* OTUs occurs at a minimum of 14% FD and broadly distinguishes two groups, an 'eastern' and a 'western' group. These two groups show diagnostic allozyme differences at four loci (*Ada, Dia, Gda* and *Iddh*) and other differences that are diagnostic for some of the OTUs between each group at eight loci (*Aat-2, Acoh-1, Acoh-2, Acyc, Fumh, Pep-A, Pep-B1* and *Pep-D*). There is genetic divergence within both the 'eastern' and 'western' groups with seven loci (*Acoh-2, Acyc, Dia, Gox, Mpi, Pep-B2* and *Pep-D*) displaying fixed allelic differences between one or more OTUs in the 'eastern' group and six loci (*Acoh-1, Acoh-2, Eno, Iddh, Pep-B1* and *Pep-D*) displaying fixed allelic differences between one or more OTUs in the 'western' group. The greatest intragroup genetic divergence, at an average of 10% FD, is between the OTUs WIN, WID and COR from central Queensland (Qld) and the 'eastern' group OTUs situated in the corridor between the eastern and western deserts. This may reflect the well-known climatic-ecological barrier of the Simpson Desert on patterns of speciation (Cracraft 1986, 1991).

None of the OTUs of the 'eastern' and 'western' groups were found in strict sympatry. However, 'eastern' and 'western' groups were found in regional sympatry, i.e. within 30–80 km of each other, in the Coober Pedy/Mabel Creek area (OTUs COO and MAB). Fixed allelic differences at six loci (*Ada, Dia, Gda, Iddh, Pep-A* and *Pep-B2*) were found between the two OTUs. Given the null hypothesis that two OTUs are sampled from a single population of eight individuals, the probability of not observing a heterozygote at the six loci showing fixed allelic differences can be derived from the Hardy-Weinberg equation as $(1-[2 \times 0.125 \times 0.875])^{6 \times 8} = 7.035 \times 10^{-6}$ (see Richardson *et al.* 1986 for a fuller explanation of this approach). Hence, the null hypothesis can be rejected and a reasonable alternative hypothesis is that two species are present in the Coober Pedy/Mabel Creek area.

A second split among the *P. nigriceps* OTUs occurs at a minimum of 21% FD and distinguishes

the 'eastern' and 'western' groups from a single 'northern' OTU, CAP. There are diagnostic allozyme differences between the 'eastern' and 'northern' groups at six loci (*Acoh-2, Acyc, Ada, G3pdh, Pep-B1*, and *Sod*) and between the 'western' and 'northern' groups at five loci (*Acyc, Dia, G3pdh, Iddh* and *Mpi*). In addition, there are other differences that are diagnostic for some of the OTUs between the 'northern' and other two groups at 11 loci (*Acoh-1, Acoh-2, Dia, Gda, Iddh, Mpi, Pep-A, Pep-B1, Pep-B2, Pep-D* and *Sod*).

The magnitude of the genetic differences encountered, the evidence of separate evolutionary histories of the 'eastern', 'western' and 'northern' groups and direct evidence of lack of gene flow between two of the lineages is sufficient to reject the null hypothesis of a single species within *P. nigriceps*. Consequently, we considered the groups as three separate species for the purposes of morphological examination. The 'eastern' and 'western' groups correspond roughly in

geographic location with Kluge's (1974) suggested ranges for *P. n. schraderi* and *P. n. nigriceps* respectively. The 'northern' group comprises only one population in the samples available for electrophoresis thus preventing any delineation of its geographical distribution on allozyme data alone. These three groups proved to have a distinctive suite of morphological characters as outlined in the following analysis.

A summary of the variation in morphological characters is shown in Table 2 for the three groups. The data in Table 2 show that a suite of morphological features varies concordantly with the electrophoretic data. This table therefore provides the basic morphological characters for separating specimens into the 'eastern', 'northern' and 'western' groups.

The 'western' group is easily separated from the other two groups in that: the nostril is separated from the first supralabial scale by the nasal ('subnasal scale' present); dorsal scale keeling is absent; the mean number of ventral

TABLE 2. Morphological statistics for specimens of *Pygopus* for which allozyme data were collected. E = 'eastern' group, N = 'northern' group, W = 'western' group. See text for character abbreviations. $\bar{x}$ = mean, $S$ = standard deviation, $R$ = range, $n$ = sample size, * $P$ for two-tailed Mann-Whitney $U$ or unpaired Student's $t$ tests, tests for normal distribution[n] and equality of variances[v] were not significant. See Materials and Methods for the definitions of characters.

| Character | Group | Univariate Statistics | | | Pairwise Statistical Comparisons* | | |
|---|---|---|---|---|---|---|---|
| | | E ($n$=11) | N ($n$=3) | W ($n$=26) | E/N | E/W | N/W |
| SNS | $\bar{x}$ ($S$) | 0 (0) | 0 (0) | 1 (0) | 0.88 | <0.001 | <0.001 |
| VS | $\bar{x}$ ($S$) | 110.3 (4.6) | 109.7 (1.2) | 130.8 (5.9) | 1.0 | <0.001 | <0.001 |
| | $R$ | 105–122 | 109–111 | 114–140 | | | |
| OS | $\bar{x}$ ($S$) | 9.18 (1.17) | 10.7 (1.5) | 11.8 (1.6) | 0.17 | <0.001 | 0.35 |
| | $R$ | 7–11 | 9–12 | 10–16 | | | |
| DSK | $\bar{x}$ ($S$) | 2(0) | 1(0) | 0(0) | 0.005 | >0.001 | <0.001 |
| DSRK | $\bar{x}$ ($S$) | 12.4 (0.8) | 7.67 (1.58) | 0 (0) | 0.005 | >0.001 | <0.001 |
| | $R$ | 12–14 | 6–9 | | | | |
| PP | $\bar{x}$ ($S$) | 13.0 (1.2) | 13.3 (0.6) | 10.2 (1.1) | 0.45 | <0.001 | <0.001 |
| | $R$ | 12–15 | 13–14 | 8–12 | | | |
| DIP | $\bar{x}$ ($S$) | 0.45 (0.52) | 0.33 (0.58) | 2.32 (.80) | 0.78 | <0.001 | 0.004 |
| | $R$ | 0–1 | 0–1 | 0–3 | | | |
| DNP | $\bar{x}$ ($S$) | 2.09 (0.83) | 1.33 (1.15) | 2.92 (0.28) | 0.29 | 0.001 | 0.002 |
| | $R$ | 0–3 | 0–2 | 2–3 | | | |
| OP | $\bar{x}$ ($S$) | 1.91 (0.70) | 2.67 (0.58) | 2.44 (0.71) | 0.37 | 0.09 | 0.89 |
| | $R$ | 1–3 | 2–3 | 1–3 | | | |
| NP | $\bar{x}$ ($S$) | 1.82 (0.60) | 0 | 1.2 (1.04) | 0.005 | 0.02 | 0.06 |
| | $R$ | 1–3 | – | 0–3 | | | |
| LHP | $\bar{x}$ ($S$) | 1.09 (0.30) | 3.67 (0.58) | 2.24 (0.88) | 0.005 | <0.001 | 0.019 |
| | $R$ | 1–2 | 3–4 | 1–4 | | | |
| SVL | $\bar{x}$ ($S$) | 147.6 (23.1)[n] | 136.0 (7.9)[n] | 156.1 (33.2)[n] | 0.42[v] | 0.45[v] | 0.31[v] |
| | $R$ | 96–178 | 130–145 | 79–204 | | | |

scales is greater than 120; the mean number of preanal pores is less than 12; there is usually a well-developed blackish interorbital bar.

The 'eastern' group can be separated from the 'northern' group in that: The dorsal scales are moderately keeled with keeling occurring over ten or more rows in the 'eastern' group but weakly keeled over fewer than ten rows in the 'northern' group. The orbital and narial patches are present and are of moderate and equal intensities in the 'eastern' group, while in the 'northern' group the orbital patch is more strongly expressed than the nasal patch in any individual, and the nasal patch may be completely absent.

These characters were then used to separate the museum specimens for which tissues had not been available for allozyme electrophoresis. The great majority of specimens were readily separated (n = 251) but some difficulty was experienced in separating six 'eastern' and 'northern' specimens that had 'washed out' body patterns together with indeterminate scale keeling. The consistent allozyme and morphological differences between

the three groups is sufficient for each group to be given species status. The 'western' group is *P. nigriceps*, the 'eastern' group *P. schraderi* and the 'northern' group *P. steelescotti* sp. nov. A map showing the geographic distribution of the three species is shown in Fig. 3. Note that the distributions of *P. nigriceps* and *P. schraderi* overlap in south-western Queensland (Qld), eastern NT and central and eastern SA; and those of *P. nigriceps* and *P. steelescotti* sp. nov. overlap in northern NT and WA; and all three species are found in eastern NT.

Once separated into the three species, the characters used in the morphological study on the electrophoresed specimens were scored. The results are summarised in the species descriptions given below. An additional character of Kluge, tail length, was added. It was measured as the horizontal distance between the posterior-most extreme of the middle preanal scale and the tip of the tail. Measurements were made only on those few specimens with complete and unregenerated tails.
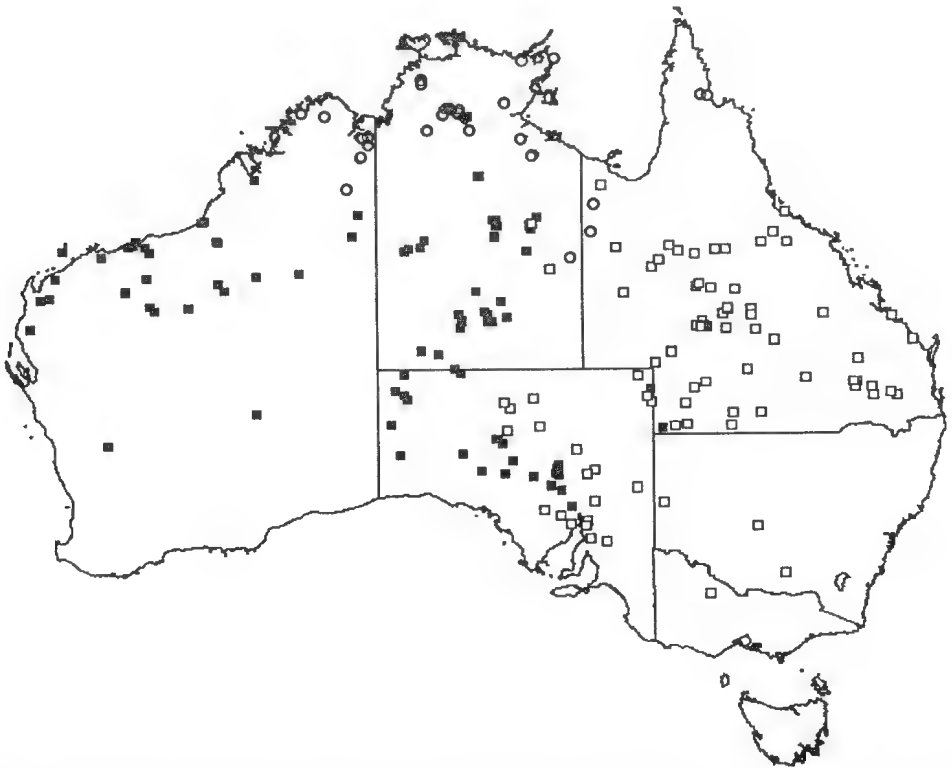


FIGURE 3. Map showing geographic distribution of specimens of *Pygopus* examined for morphological characters. ■ = *P. nigriceps*, ◯ = *P. steelescotti*, ▢ = *P. schraderi*.

The *P. nigriceps* species complex conforms to Kluge's (1976) definition of the genus *Pygopus*. The dorsal surface of the head is covered with large and small scales, there are between three and five postmental scales, 21 or more midbody scale rows, nine or more preanal pores and the dorsal body scales are often keeled. The three species of the complex differ from the only other species in the genus, *P. lepidopodus*, in that the *P. nigriceps* complex has immaculate ventral surfaces (versus boldly variegated with black), smooth to moderately keeled dorsal scales (versus strongly keeled) and there is no dorsal snout pattern.

## *Pygopus nigriceps* (Fischer, 1882)

*Cryptodelma nigriceps* Fischer, J. G. (1882), p. 290. Holotype SMNS 2259, Nickol Bay, WA. Type lost, believed destroyed during World War II (Schlüter and Hallermann 1997).

*Delma (Cryptodelma) baileyi* Günther, A. (1897), p. 170. Holotype BMNH specimen, now lost (Kluge 1974), from the neighbourhood of Cue, WA.

*Pygopus territorianus* Wells, R. W. and Wellington, C. R. (1985), p. 16. Holotype AMS R56823, near Tennant Creek, NT.

### Notes

Both of the names that could be applied to the 'western' species are based on type specimens that are now lost. Fortunately, both have fairly precise type localities, which place them well outside the known distribution of the other two species. *Cryptodelma nigriceps* was described and figured by Fischer (1882) who proposed the new genus for this species, which appeared to combine the smooth scalation of *Delma* with preanal pores as in *Pygopus*. Fischer acknowledged that his very small specimen (SVL 64 mm) was almost certainly a juvenile, and its SVL is smaller than any we measured, although we did not extensively sample juveniles. The illustrations clearly depict the V-shaped preanal pore row (11 pores), large hindlimb flaps and head scalation (form of the two frontal shields and double row of loreal scales), a combination of features confined to *Pygopus* (*sensu* Kluge 1974). The dark head and nape markings are described and figured as confluent, unusual in specimens of the 'western' species but not unknown (e.g. SAMA R22932 from Barradale, WA).

Günther (1897) described his new species, *Delma (Cryptodelma) baileyi*, from an immature specimen (SVL 90 mm), noting that it was very close to Fischer's *nigriceps* but differed in its lower midbody scale count (22, versus 26 or 28). Fischer, however, implicitly included the ventrals in his midbody count, making his specimen's likely dorsal count 24 or 26, 24 being a frequent count in WA specimens. As with *C. nigriceps*, Günther's specimen had smooth scales and 11 preanal pores, both characteristic features of the 'western' group. Günther's illustration shows distinct black interorbital and nuchal colouring, with blackish narial and orbital patches extending on to the lower labials again features typical of the 'western' species.

Wells and Wellington (1985) proposed *Pygopus territorianus* as a new species from the Northern Territory, but provided little justification. They stated that this species could be 'readily diagnosed by consulting existing descriptive references' and the figure of a typical specimen (possibly the holotype) in Swanson (1976; Pl 34). They also added that the species lacks the distinctive keeling of the body scales seen in *Pygopus klugei* (*q.v.* = *P. schraderi*) and lacks the colour pattern ('reticulated patterning') of *P. schraderi*. The holotype is a specimen of the western form, and we therefore regard *P. territorianus* as a junior synonym of *C. nigriceps*. The body scales are completely smooth, the nostril is separated from the first upper labial and there are 11 preanal pores. The ventral count is relatively low (120) for the western form, but still within the sample range, and the colour pattern is markedly 'faded', with little black pigment remaining on top of the head, a trend in some populations of all of the *P. nigriceps* complex. The tail shows the strong pattern of dark-edged scales typically present in the 'western' form.

### Neotype

To stabilise the name, a neotype, WAM R102063, has been selected for *Cryptodelma nigriceps*, from the same geographical area as the lost type (see notes). It was collected on the Yule River, WA (20°40'S, 118°21'E) by D. Robinson in 1990.

### Diagnosis

A large pygopod (SVL up to 227 mm.) differing from other *Pygopus* in having smooth dorsal scales, the nostril entirely contained within the nasal, usually 120 or more ventral scales, and fewer than 14 preanal pores.
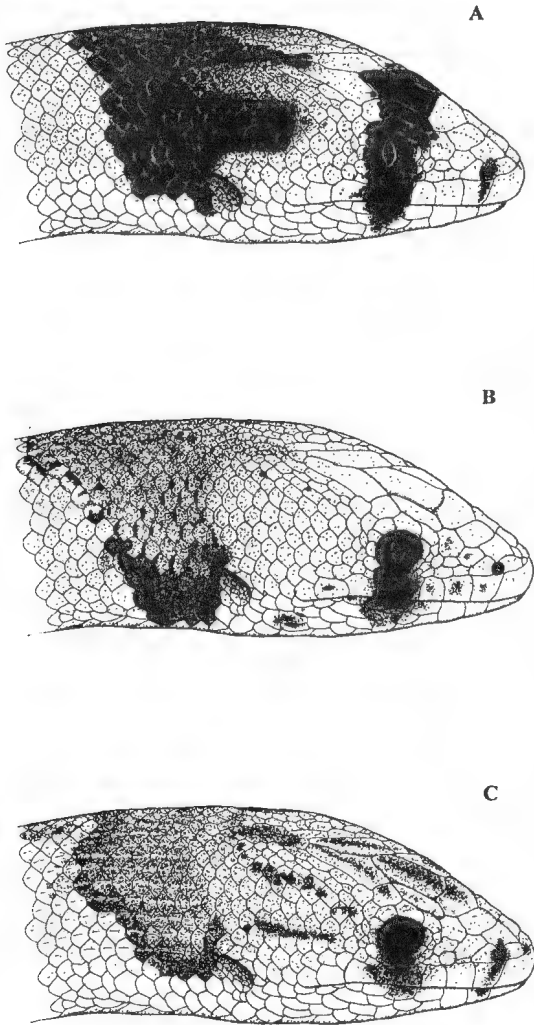
A

B

C

FIGURE 4. Representative head patterns of three species of *Pygopus*: (A) *P. nigriceps* (SAMA R48749); (B) *P. steelescotti* (NTM R20546); (C) *P. schraderi* (SAMA R46370).

*Description*

Ventral scales 114–143 ($\bar{x}$ = 130.0, $S$ = 5.9, $n$ = 116); orbital scales 9–16 ($\bar{x}$ = 11.6, $S$ = 1.4, $n$ = 118); nostril always completely enclosed by the nasal, separated from first supralabial scale ($n$ = 119); preanal pores 8–14 ($\bar{x}$ = 10.8, $S$ = 1.1, $n$ = 117); snout-vent length 73–227 mm ($\bar{x}$ = 157.6, $S$ = 33.7, $n$ = 118); tail length ranges from 104% of SVL in smallest juveniles to 165% of SVL in largest specimens; no dorsal scale keeling ($n$ = 118).

*Colouration*

In preservative, the basic head, body and tail colour is light tan to reddish brown. Scales, except for ventral scales, are speckled with brown or black pigmentation. Head, body and tail patterns are caused by the relative intensities and widths of the pigmented scale margins or by individual paler and darker speckled scales. Head patterns are formed with brown to black pigmentation and body and tail patterns by light to dark brown pigmentation. Ventral surfaces are immaculate with the scales a creamy-white or silver colour. There is a dark brown or black pigmented bar present on the dorsal surface of the head between the orbits which extends as a teardrop-shaped orbital patch descending to the supralabial scales and sometimes to the infralabial scales (Fig. 4A). A further area of dark pigmentation, but less intense, is found around the nostrils, again extending to the supralabial scales and sometimes to the infralabial scales. A brown to black nuchal band extends to the ear openings. There is no distinct body patterning. The tail is marked, often strongly, in the form of dark brown backward pointing chevrons that converge on the vertebral line. The smallest juveniles (SVL about 75 mm) are sandy-yellow with low levels of scale pigmentation except for the heavily black pigmented and contrasting head pattern. There is no distinct body pattern in juveniles and only weak light-brown chevrons on the tail. Coloration in life is shown in photographs in Storr *et al.* (1990: Pl 20, Figs 3–4), Glasby *et al.* (1993: Pl 4, Fig. 12), Cogger (1996: p. 297).

*Distribution*

West of 136°E and the far south-western corner of Queensland (Qld) (Fig. 3).

**Pygopus schraderi** Boulenger, 1913

*Pygopus schraderi* Boulenger, G. A. (1913), p. 564. Holotype BMNH 1946.8.27.2 (formerly 1913.7.28.2), collected at Milparinha [*sic* = Milparinka], NSW by P. Schrader.

*Pygopus klugei* Wells, R. W. and Wellington, C. R. (1985), p. 16. Holotype AMS field series 28686 (now registered as AMS R116980), 6.2 km S of Big Warrambool, NSW.

*Notes*

The holotype specimen is in good condition, with the colour pattern still readily discernible. It has an equal development of the orbital and narial

patches, but the interorbital area is only weakly pigmented. Although very young (SVL 65 mm), it has distinct low keels on the dorsal scales. There are 14 preanal pores. Boulenger (1913) gave the ventral count as only 97 pairs (enlarged scales only); the ventral count using our (Kluge's) method is 109. The characteristics of the type are completely concordant with the 'eastern' species in the complex.

Wells and Wellington's (1985) *Pygopus klugei* is a junior synonym of *P. schraderi*. The holotype specimen has 12 dorsal scale rows with distinct keels, there are 102 ventrals and the nostril contacts the first supralabial. There is a complex colour pattern on head body and tail, including well developed eye and nostril patches. Wells and Wellington were clearly influenced by the purported lack of keeling of the holotype of *P. schraderi*, a persistent misapprehension due to the rudimentary keeling in juveniles, including the holotype. Two illustrations said by Wells and Wellington to be *P. schraderi* (Cogger 1983; plates 104 and 495) show, respectively, a juvenile *P. nigriceps* and an adult *P. schraderi*.

### Diagnosis

A large pygopod (SVL up to 198 mm) having unicarinate dorsal scale keeling extending over 10 or more rows, dark teardrop-shaped patches under both the orbits and nostrils, fewer than 120 ventrals, usually 13 or more preanal pores, nostril always in contact with the first supralabial scale and often strongly marked body and tail patterning.

### Description

Ventral scales 100–122 ($\bar{x}$ = 109.4, $S$ = 4.9, $n$ = 85); orbital scales 6–13 ($\bar{x}$ = 9.87, $S$ = 1.27, $n$ = 85); nostril always in contact with first supralabial scale ($n$ = 92); preanal pores 11–17 ($\bar{x}$ = 13.8, $S$ = 1.4, $n$ = 85); snout-vent length 70–198 mm ($\bar{x}$ = 142.6, $S$ = 29.4, $n$ = 91); tail length ranges from 99% of SVL for smallest juveniles to 170% of SVL for the largest specimens; dorsal scale rows with either weak or moderate keeling, usually moderate (80%), ($\bar{x}$ = 1.88, $S$ = 0.28, $n$ = 86) extending over 9–14 dorsal rows ($\bar{x}$ = 11.7, $S$ = 1.8, $n$ = 86).

### Colouration

In preservative, the scales are pigmented in a manner similar to *P. nigriceps*. The background colour of the head, body and tail can vary from light tan to dark grey. The head is usually of mottled appearance. Head patterning is similar to that of *P. nigriceps* except that there is no pigmented band on the dorsal surface of the head between the orbits, the relative intensities of the pigmented bands below the orbits and nostrils are approximately equal and the nuchal band is frequently indistinct (Fig. 4B). Often, there is a strongly marked body pattern in the form of a longitudinal series of light or dark brown uniformly pigmented scales on the dorsal surface and upper flanks giving the impression of discrete broken lines. Many individuals have an almost continuous stripe along the vertebral line. On the lower flanks is a similar series of discrete broken lines caused by a scattering of creamy-white scales. The tail patterning is in the form of narrow crossbands (occasionally posteriorly pointing chevrons converging on the vertebral line). The body patterning is caused by individual scales of differing levels of pigmentation whilst the tail patterning is caused by scale margin pigmentation. The intensity of patterning is very variable with many specimens being strongly marked, others having a light tan overall colour and a washed-out appearance, whilst still others are heavily pigmented all over. Body patterning does not appear to be geographically correlated. The smallest juveniles are similar in size and colouration to those of *P. nigriceps*. Head patterns are pronounced and are brown or black. There is no distinct body pattern and only weak light brown crossbands or chevrons on the tail. There is weak dorsal scale keeling.

Colouration in life is shown in photographs in Wilson and Knowles (1988: Fig. 263), Swan (1990: p. 47), Ehmann (1992: p. 102).

### Distribution

East of 135°E, south of 17°S and west of the Great Dividing Range in New South Wales and Victoria (Fig. 3).

### *Pygopus steelescotti* sp. nov.

### Holotype

NTM R20546, collected at Cape Crawford, NT (16°34.3'S, 135°57.9'E) by P. Horner, 1994.

### Diagnosis

A large pygopod (SVL up to 185 mm) similar to *P. schraderi* except for weaker unicarinate dorsal scale keeling usually extending over less than 10 rows and a less complex color pattern,

with a dark orbital patch but no or very weak nasal patch.

## Description

Ventral scales 103–125 ($\bar{x}$ = 114.2, $S$ = 4.8, $n$ = 43); orbital scales 7–13 ($\bar{x}$ = 9.86, $S$ = 1.10, $n$ = 43); nostril always in contact with first supralabial scale ($n$ = 44); preanal pores 12–17 ($\bar{x}$ = 14.0, $S$ = 1.0, $n$ = 43); snout-vent length 79–185 mm ($\bar{x}$ = 139.0, $S$ = 24.2, $n$ = 43); tail length ranges from 100% of SVL for smallest juveniles to 152% of SVL for the largest specimens; dorsal scale rows keeling either absent or weak, usually weak (86%), ($\bar{x}$ = 0.86, $S$ = 0.35, $n$ = 44) extending over 0–13 dorsal rows ($\bar{x}$ = 7.1, $S$ = 3.46, $n$ = 44).

## Colouration

In preservative, the background head, body and tail colour is light tan to sandy-yellow with patterns similar to those found on the less heavily patterned individuals of *P. schraderi*. There is often no pigmentation around and below the nostrils; if it is present it is usually faint in intensity compared to the teardrop below the orbits (Fig. 4C). Many specimens are light tan in colour and have a washed out appearance and, unlike *P. schraderi,* there are no strongly patterned or darkly coloured specimens. The smallest juveniles are similar to those of *P. schraderi* differing only in the head pattern and in having no (or extremely weak) dorsal scale keeling. Colouration in life is shown in photographs in Wilson and Knowles (1988: Fig. 264) and Ehmann (1992: p. 101).

## Etymology

The species is named in honour of the late Dr Colin Steele-Scott, a keen supporter of the South Australian Museum.

## Distribution

North of 22°S in NT, Qld and WA (Fig. 3).

## Discussion

When considered as a single species, the concept of *P. nigriceps* that existed prior to this study was of an extremely successful, ecologically generalised arid zone lizard, adapted to a broad habitat range. The three species that we now recognise are each more restricted ecologically, as well as geographically. *Pygopus nigriceps* (*s.s.*) is primarily a sandy desert species, at least in Central Australia. *Pygopus schraderi* occupies a range of habitats, and while it has been recorded from sandy terrain (e.g. far eastern S.A.) it is typically found on rocky hillsides or clayey or stony flats. *Pygopus steelescotti* is less well-known with respect to habitat selection but differs again in being confined to the wet-dry tropical belt across northern Australia.

All three species in the complex may be strictly nocturnal, relatively unusual in pygopods, most of which engage in significant diurnal activity (Shea 1993). Field experience with both *P. nigriceps* and *P. schraderi* in South Australia indicates that specimens are only seen actively foraging at night, and pitfall trapped individuals are taken only overnight, not by day (M. Hutchinson pers. obs.).

Of the three species, *P. nigriceps* is the most easily identified, based on its completely smooth dorsal scalation, the nostril completely contained by the nasal, and the high ventral and low preanal pore counts. By contrast, the other two species are very similar, exacerbated by the tendency of geographically proximate populations of *P. schraderi* to be the most weakly patterned and therefore most similar to *P. steelescotti*. The similarity of *P. schraderi* and *P. steelescotti* is such that specimens from the potential area of contact along the southern margin of the wet-dry tropics in the NT and Qld should be carefully checked. At present, *P. steelescotti* seems consistently identifiable by the lower number of keeled dorsal scale rows (usually nine or fewer), weakly developed keeling on dorsal scale rows and differential development of the dark nasal (absent or weak) and orbital (moderately well developed) patches.

Further taxonomic work will be useful to help in defining the variation and degree of sympatry of the three dark-headed species of *Pygopus*. Taxonomic work is also further warranted on the northeastern Qld populations of *P. lepidopodus*. Based on our samples, the Cooktown specimen appears to be completely distinct from the more southerly populations, which themselves show some heterogeneity in morphology and electrophoretic markers. The status of the eastern Australian *P. l. squamiceps* Gray is yet to be properly assessed.

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Museum registration numbers for *Pygopus* specimens examined. The superscript \* denotes specimens which were used in the electrophoretic study. The superscript # denotes specimens used in the electrophoretic study where the body was not available for morphological analysis. Abbreviations in bold upper case refer to OTUs designated in the allozyme electrophoresis analysis. Institutional acronyms (underlined) follow Leviton *et al.* (1985) and ABTC = Australian Biological Tissue Collection, South Australian Museum.

*Pygopus nigriceps*: AMS R60245–6. NTM CAMR531, NTM R30, R157–8, R291–3, R321, R444, R829, R905, R1427–8, R1630, R2209, R2216, R2356, R2532, R3228, R3316, R5314, R5907, R6387, R7092, R9530, R9691–6, R9701, R9703, R9808, R14021, R15153*(**TAN**—30 km SW Sangster's Bore, Tanami Desert, NT), R17571, R18058, R18079, R20670*(**FIN**—Finke Gorge National Park, NT). QM J28440, J33389. SAMA ABTC6588*#(**MAB**—Mabel Creek Station, SA), ABTC31799*#(**MAC**—MacDonnell Ranges, NT), ABTC31812*#(**MAC**), R600, R876, R4791, R8116, R12911, R15548, R16279, R16768, R17459, R19251, R20711*(**OLY**—Olympic Dam, SA), R21029/33*(**OLY**), R21035, R22932–3*(**BAR**—8 km S Barradale, WA), R23197*(**LAV**—134 km ENE Laverton, WA), R23908*(**LAV**), R26198–200*(**MAB**), R26202*(**MAB**), R26222*(**MAB**), R26385, R26646, R26686*(**MAB**), R28546*(**BOO**—near Boologooroo Homestead, WA), R33824, R34003*(**NIN**—Ninghan Homestead, WA), R36152*(**YUL**—Yulara, NT), R36169*(**YUL**), R37139, R38785–6*(**TCK**—Tennant Ck, NT), R38824*(**TCK**), R38841*(**GLE**—near Glen Helen, NT ), R42026*(**ILL**—21 km WSW Illintjitja, SA), R45264, R48608, R48668, R48749, R48765, R48792, R48830, R48928, R49156, R49310. WAM R5328, R5329, R13350, R19239, R26071–2, R30930, R36327, R40238, R52727, R64002, R64704, R69525, R73631, R73842, R75119, R75143, R79010–1, R81513, R82599, R83574, R94761, R95028, R94957*(**CAN**—Canning Stock Route, WA), R95670, R102055, R102061, R102063*(**YLE**—Yule River, WA), R103677.

*Pygopus schraderi*: AMS R6691, R8974–5, R26083, R65966. NTM R31, R8526. QM J11029, J1266, J2917, J2918, J5092, J5238, J7282, J7288, J7473, J7489, J7919, J8008, J8436, J8882, J9116, J9241, J13010, J13028, J13560, J21444, J21965, J22714, J23319, J23677, J24988, J25386, J33390, J33391, J33392, J33393, J33394, J33395, J35362, J37060, J40323, J40701, J40717, J44420, J44711, J44942, J46952, J48459, J51198, J51527, J51717, J52546, J52547, J52778, J52863, J54617, J54618, J54900, J55109, J57197, J57228, J58079, J5921, J59359, J59931, J61825. SAMA R2234, R4996, R5051, R5386, R5397, R5626, R5893, R9860, R11752, R16712, R23120*(**RM1**—Mt Remarkable National Park, SA), R23269*(**RM1**), R28389*(**IRO**—25 km NW Iron Knob, SA), R28927, R30403*(**COO**—25 km NNW Coober Pedy, SA), R40948*(**MID**—Middleback Homestead, SA), R42131, R42750*(**WIN**—15 km S Winton, Qld), R42947*/63*(**WID**—85 km W Windorah, Qld), R44808*(**COR**—Cordillo Downs, SA), R46247*(**ARC**—17 km NNE Arckaringa, SA), R46370*(**CAL**—Callana Station, SA), R46786, R48303, R49061, R49087. BMNH 1946.8.27–2.

*Pygopus steelescotti*: AMS R13233, R17981, R26579, R80336, R133267. NTM R99, R370, R821, R828, R830, R2270, R2271, R3790, R4730, R5033, R5280, R5303, R6423, R6677, R6704, R6777, R11247, R12416, R20513*(**CAP**—Cape Crawford, NT), R20545*–6*(**CAP**), R20588, R22333. QM J39061, J52746. SAMA R3510, R8117. WAM R23792, R56304, R70079, R70085, R70339, R75537–8, R83195, R83575, R87307, R99201, R101361.

*P. lepidopodus*: QM J47145*(**CTN**—Shipton's Flat, Qld). SAMA R33291*(**SYD**—Terry Hills, NSW), R20865*(**STO**—Stony Point, SA), R23629*(**RM2**—Mt Remarkable National Park, SA), R25341*(**HAM**—Hambidge Conservation Park, SA), R25689*(**YAL**—Yalata, SA), R30270*(**ESP**—Esperance, WA). WAM R77939*(**WAL**—Walpole-Nornalup National Park, WA), R90119*(**KAR**—Karridale, WA).